ISSN 1995-4255, Contemporary Problems of Ecology, 2017, Vol. 10, No. 3, pp. 259–270. © Pleiades Publishing, Ltd., 2017.
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Taxonomic Composition and Species Diversity of Insect Assemblages in Grass–Shrub Cover of Peat Bogs in Belarus

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Received March 8, 2016; in final form, October 10, 2016

Abstract—The species composition and diversity of insect assemblages in the grass–shrub cover has been studied. A total of 374 species from 10 orders have been revealed. Coleoptera, Diptera, Heteroptera, and Auchenorryncha prevailed. Each order was dominated by two to eight species. These species are *Cixius similis* Kirschbaum, 1868; *Neophilaenus lineatus* (Linnaeus, 1758); *Lepyronia coleoptrata* (Linnaeus, 1758) (Auchenorryncha); *Lygus pratensis* (Linnaeus, 1758); *Kleidocerys resedae* (Panzer, 1797); *Stictopleurus crassicornis* (Linnaeus, 1758) (Heteroptera); *Lochmaea suturalis* (Thomson, 1866); *Cyphon padi* (Linnaeus, 1758); *Plateumaris discolor* (Herbst, 1795) (Coleoptera); etc. The assemblages were characterized by low species diversity and distribution of species abundance. The most similar entomocomplexes were those in biotopes dominated by herbs, on the one hand, and dwarf shrubs, on the other. The regression analysis has shown a significant relation between the species richness and diversity of insects and the species composition of plants and their projective cover. The multivariate analysis with various methods (CCA and PCA) demonstrated the influence of these factors on the spatial distribution of certain species and their preferences to particular habitats.

Keywords: insects, peat bogs, herb-dwarf layer, taxonomic layer, species diversity, Belarus

DOI: 10.1134/S1995425517030106

INTRODUCTION

Peat bogs of Europe, including in the Republic of Belarus, are island ecosystems with specific ecological conditions that are uncommon for the temperate zone. Their plant cover is dominated by sphagnum mosses and ericaceous dwarf shrubs. Soils (peat) here are characterized by low mineralization and high acidity (Pidoplichko, 1961; Boch and Mazing, 1979). Air temperature varies greatly throughout the day. These conditions determine the specifics of animal communities in these regions. Furthermore, peat bogs are the most vulnerable ecosystems of Europe. Their area reduced significantly over the 20th century. In some regions, they have almost disappeared (Joosten and Clarke, 2002).

In Belarus, mainly Poozer'e, large bog massifs are over 10000 years old and considered the most ancient ecosystems (Pidoplichko, 1961; Gel'tman, 1982). On the other hand, many of them remain almost intact. Therefore, studying their biodiversity is important for both faunistic monitoring and understanding the evolutionary aspects and ecological mechanisms of functioning of these ecosystems.

Insects are the largest group of animals on peat bogs. They are characterized by a high ecological importance as first- and second-order consumers contributing significantly to substance and energy distribution at different levels of the trophic pyramid. Due to their high abundance and taxonomic diversity, insects are very sensitive to changes in the ecological conditions. Some highly specific species may be used as bioindicators and for monitoring purposes. The species complexes of insects, along with plant communities, may demonstrate the specifics of ecological conditions of peat bogs, Changes in their species diversity, including the evenness of species based on abundance and dominance concentration, in a number of biotopes indicate the heterogeneity of bog biotopes.

Furthermore, peat-bog ecosystems of Belarusian Poozer'e, as the least transformed in Europe, preserve the genetic pool of rare and endangered species, such as cold-loving subarctic and boreal insects (Spitzer and Danks, 2006), most of which are highly specialized and involved in the groups of tyrphobionts and tyrphophiles (Peus, 1928). The latter, owing to the specifics of ecological conditions on peat bogs, may form local populations in Belarusian Poozer'e far beyond their main habitat.

The first specific studies on insects inhabiting European peat bogs, the results of which were published in the early 20th century, cover a wide spectrum of taxa and demonstrate the specificity of their population. That period was marked by the most detailed

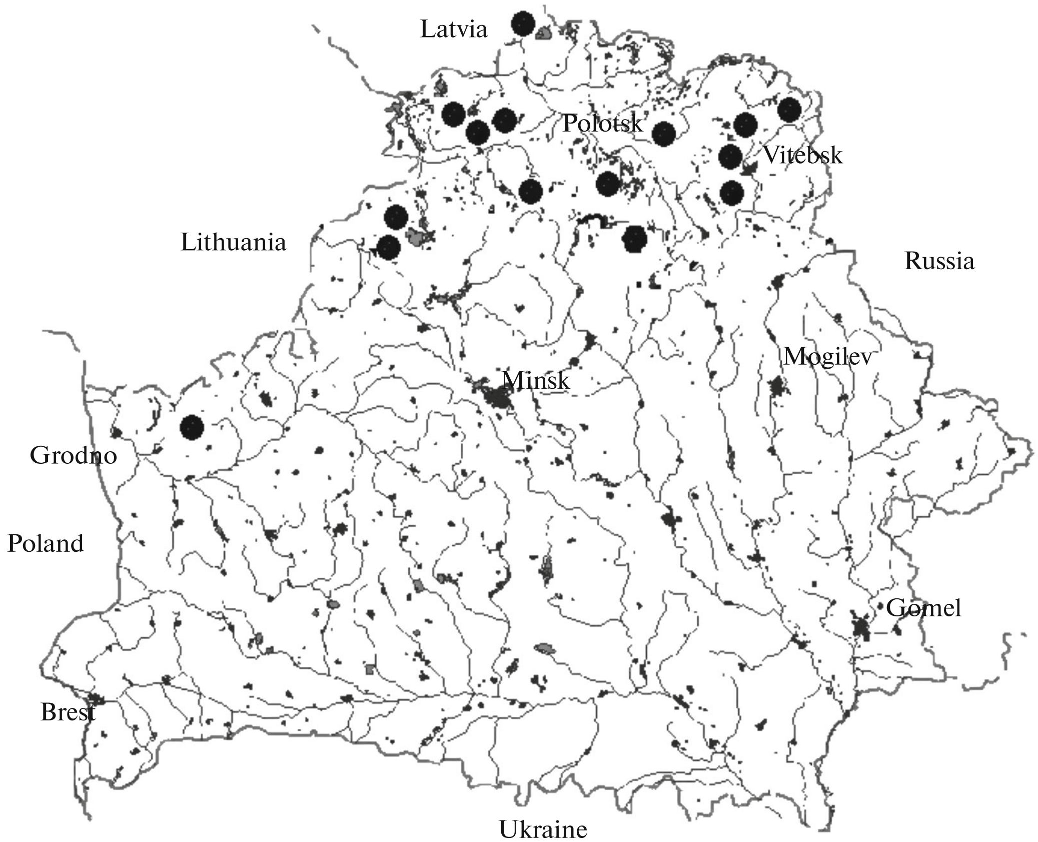

Fig. 1. Localization of the studied peat bogs in the Republic of Belarus.

summaries proceeding data on all insect orders from peat bogs in (Peus, 1928; Rabeler, 1931; Maavara, 1957; Krogerus, 1961). However, only some groups of insects, such as lepidopertans and coleopterans of the moss cover, have been well-studied in the recent period. The number of publications on insects of the herb-dwarf layer is restricted (Freese and Biedermann, 2005; Nickel and Gärtner, 2009; Rampazzi and Dethier, 1997; Montagna et al., 2008; Friess and Korn, 2013; Holzinger and Schlosser, 2013). They mainly provide data on large taxa like cycads and hemipterans. Among the most recent research, the most comprehensive study including a review of many insect taxa is the monograph on terrestrial invertebrates on peat bogs of Latvia (Spungis, 2008).

Thus, the aim of this work is to study the species composition and diversity of insect communities in the herb-dwarf shrub layer, as well as the factors determining their differentiation.

MATERIALS AND METHODS

This study was performed in the territory of Belarusian Poozer'e. The factual material (insects) was collected under field conditions on 15 peat bogs of 13 administrative districts in 2008–2015 (Fig. 1).

The main stations where long-term decade records were performed are the following bog massifs: El'nya (55°34′ N, 27°55′ E), Osveiskoe (56°5′ N, 28°7′ E), Obol' 2 (55°25′ N, 29°22′ E), and Boloto Mokh (55°37′ N, 28°06′ E). Here we performed records every decade during several field seasons. Materials from other bogs were collected several times during the field season.

The bog massif has a concentric structure in accordance with spatial differences of the peat bed. Its surface is convex and divides into a slope and a flat top (plateau). The bog is surrounded with a transition zone: margin (lagg zone) (Fig. 2).

The stations for material collection were singled out from the edge to the top of the bog in accordance to the gradient of ecological conditions. Plant associations were named based on the dominant system of syntax using comprehensive reviews on the classification of peat bogs as the main sources (Pidoplichko, 1961; Boch and Mazing, 1979).

The seven most typical biotopes were singled out for investigation: (1) lagg zone (LZ): it stretches as a narrow band along the bog margin, borders the adjacent biocenoses on mineral soils; the LZ is characterized by significant fluctuations in the level of bog waters and, being overmoistened in early spring, plants

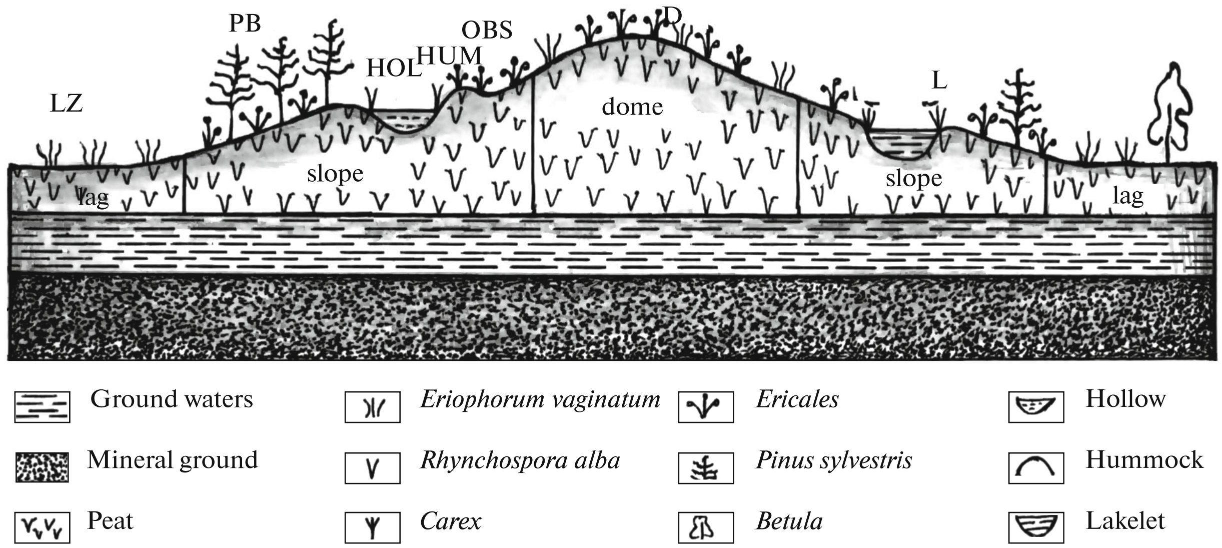

Fig. 2. Peat-bog profile and localization of sampling gounds: LZ, lagg zone; PB, sphagnum pine bogs; HOL, hollows; HUM, hummocks; OBS, open bogs on the slope; L, lakeshores; and D, open biotopes on the dome.

here are represented by cotton grass–sphagnum phytocenoses (*Eriophorum vaginatum* + *Rhynchospora alba* – *Sphagnum angustifolium*). (2) Pine bogs (PB) on the slope: they are characterized by plane landscape and relatively low water content; plants here are represented by the pine-dwarf shrub–cotton grass–sphagnum association (*Pinus sylvestris* – *Eriophorum vaginatum* – *Ledum palustre* – *Sphagnum magellanicum* + *S. angustifolium*), where the tree layer is very sparse and involves the suppresed species *Pinus sylvestris* f. *Litwinowii*. Dwarf shrubs include *Ledum palustre, Calluna vulgaris*, *Chamaedaphne calyculata, Oxycoccos palustris*, *Empetrum nigrum*; herbs are *Eriophorum vaginatum*; and mosses are *Sphagnum magellanicum*, *S. rubellum*, and *S. balticum*. (3) Hollows of the hummock-hollow complex (HOL) on the bog slope: they are distinguished by continuous overmoistening and located between the altering elevations, i.e., hummocks; plants are represented by the beak rush–sphagnum associations (*Rhynchospora alba* – *Sphagnum cuspidatum*), herbs are *Rhynchospora alba, Scheuchzeria palustris*, *Carex limosa*, *Eriophorum vaginatum*, and *Drosera rotundifolia*; dwarf shrubs are *Oxycoccos palustris* and *Andromeda polifolia*; and mosses are *Sphagnum cuspidatum, S. balticum*, and *S. rubellum*. (4) Hummocks (HUM) on the bog slope: the moisture content is low and the landscape is hummocky. Plants are represented by the dwarf shrub–cotton grass–sphagnum aasociation (*Eriophorum vaginatum* – *Oxycoccus palustris* + *Andromeda polifolia* + *Ledum palustre* – *Sphagnum magellanicum* + *S. angustifolium* + *S. fuscum*); herbs are *Eriophorum vaginatum*; dwarf shrubs are *Ledum palustre*, *Chamaedaphne calyculata*, *Calluna vulgaris, Andromeda polifolia*, *Vaccinium uliginosum, Oxycoccus palustris,* and *Empetrum nigrum*; and mosses are *Sphagnum magellanicum*, *S. fuscum*, *S. rubellum*, and sometimes *Polytrichum strictum*. (5) Open bog (OBS) on the slope: they are characterized by a leopard-spotted landscape and relaively low water content. Plants are represented by the dwarf shrub–cotton grass–sphagnum association (*Eriophorum vaginatum* – *Ledum palustre* – *Chamaedaphne calyculata* – *Empetrum nigrum* – *Calluna vulgaris* – *Oxycoccus palustris* + *Andromeda polyfolia* + *Vaccinium uliginosum* – *Sphagnum magellanicum* + *S. angustifolium* + *S. fuscum*); herbs are *Eriophorum vaginatum, Drosera* spp.; dwarf shrubs are *Ledum palustre, Chamaedaphne calyculata, Calluna vulgaris*, *Oxycoccus palustris*, and *Andromeda polifolia*; and mosses are *Sphagnum magellanicum*, *S. rubellum*, *S. fuscum,* and *S. balticum*. (6) Lakeshores (L) of the hummock–lakelet complex: they are characterized by high water content. Plants are represented by the sedge–sphagnum association (*Carex limosa* – *Sphagnum cuspidatum*); herbs are *Carex limosa*, *Eriophorum vaginatum*, *Rhynchospora alba*, and *Scheuchzeria palustris*; and moss is *Sphagnum cuspidatum*. (7) Dome (D): low water content, often with conditons of its dramatic shortage, weak hummocky landscape. Plants are represented by the dwarf shrub–cotton grass–sphagnum association (*Eriophorum vaginatum* – *Calluna vulgaris* + *Ledum palustre* – *Sphagnum fuscum* + *S. magellanicum*); dwarf shrubs are mainly *Calluna vulgaris* and extremely suppressed *Ledum palustre*, *Chamaedaphne calyculata*, and *Vaccinium uliginosum*; herbs are *Eriophorum vaginaiutn*; and mosses are *Sphagnum fuscum* and *S. magellanicum* (Fig. 2). In each biotope, three sites (50 × 50 m) with homogenous vegetation (a total of 21 sites) were studied with regard for the total projective cover (%) of plants in the layer, projective cover

Table 1. Main parameters (±SE) of the studied biotopes on peat bogs of Belarus

Environment variable	Biotopes						
	LZ	PB	HOL	HUM	OBS	L	D
Projective cover of dwarf shrubs, %	10.8 ± 2	57.9 ± 11	8.3 ± 6	54.3 ± 3	59.4 ± 16	0	56.1 ± 7
Projective cover of herbs, %	68.8 ± 6	12.1 ± 4	43.3 ± 3	19.7 ± 2	28.5 ± 18	81.9 ± 1	24.7 ± 2
General projective cover, %	79.6 ± 5	85.5 ± 2	51.6 ± 7	73.7 ± 2	87.9 ± 4	81.9 ± 2	80.8 ± 8
Height of plants	31 ± 0.27	30 ± 0.91	28 ± 0.37	23 ± 0.44	32 ± 11	38 ± 0.48	24 ± 0.97
Number of higher vascular plant species	3	10	1	8	9	1	7
Level of bog waters, cm	4 ± 0.41	12 ± 0.11	1 ± 0.07	15 ± 0.36	12 ± 0.11	1 ± 0.04	35 ± 0.47
Number of studied sites per biotope	3	3	3	3	3	3	3

LZ, lagg zone; PB, sphagnum pine bogs; HOL, hollows; HUM, hummocks; OBS, open bogs on the slope; L, lakeshores; and D, open biotopes on the dome.

of herbs (%) and dwarf shrubs (%), plant height, number of higher vascular plant species, presence of tree layer, and level of bog waters (Table 1). The areas of study were located at a distance of at least 50 m from each other.

The material was collected by entomogical sweep netting (diameter 30 cm). The unit of account is 50 sweeps with fivefold repetition. The investigations were performed from May to October.

The α diversity was evaluated using Simpson's index of dominance (D) and Shannon's diversity index (H'). The evenness of species by their abudnance was evaluated by the Pielou index (J). Hierarchical cluster analysis (UPGMA linking method) was applied to study the β diversity (Magurran, 1992).

Effects of the studied factors on the species richness and diversity of insects in the herb-dwarf shrub layer were evaluated with the help of regression analysis, based on the general linear model (GLM) in particular (Zuur et al., 2009). Principal component analysis (PCA) was used for ordination with respect to species and their habitats (Jongman et al., 1999). Using canonical correspondence analysis (CCA), a dependence of distribution patterns for some species on the environmental factors under consideration was investigated. Logarithms were taken of data on species abundance ($\log_2$). Abbreviations of species names are given on the ordinal diagrams (three initial capitals of genus and species names). Species known by 1–2 individuals were excluded from further analysis.

Calculations were performed with the help of the Past® (Hammer et al., 2001) and R 2.12.2 (R Development Core Team, 2011) software.

RESULTS

Taxonomic composition of insects in the herb–dwarf shrub layer. A total of 374 insect species from 10 orders were identified in the herb–dwarf shrub layer: Dictyoptera (1 species), Orthoptera (9 species), Psocoptera (2 species), Sternorrhyncha (7 species), Auchenorryncha (46 species), Heteroptera (75 species), Coleoptera (153 species), Neuroptera (10 species), Hymenoptera (7 species), and Diptera (64 species). Due to difficulties arising during the identification of representatives of the orders Hymenoptera and Diptera, their taxonomic position was determined to family level (see Table 2).

Most of these insects are topically and trophically associated with the herb-dwarf shrub layer, but certain actively flying species only occasionally visit it. This is especially noticeable when dwarf shrubs bloom. The common dwellers are dipterans from the suborder Nematocera, which belong to the families Tipulidae, Limoniidae, Mycetophilidae, Cecidomyiidae, Sciaridae, Culicidae, Simuliidae, Ceratopogonidae, and Chironomidae. In this group, the species composition of the families Tipulidae (7 species) and Limoniidae (11 species) was found (Paramonov and Sushko, 2010).

Among representatives of the suborder Brachycera, the species composition of the following families was revealed: Rhagionidae (1 species), Tabanidae (2 species), Empididae (5 species), Hybotidae (2 species), Dolichopodidae (5 species), Syrphidae (27 species), Chamaemyiidae (1 species), Sciomyzidae (6 species), Sepsidae (5 species), Opomyzidae (1 species), Chloropidae (9 species), Scathophagidae (4 species), Calliphoridae (1 species), and Tachinidae (9 species). Furthermore, species of the following families were collected: Stratiomyidae, Bombyliidae, Lonchopteridae, Phoridae, Pipunculidae, Conopidae, Tephritidae, Lauxaniidae, Sphaeroceridae, Drosophilidae, Ephydridae, Anthomyiidae, Sarcophagidae, and Muscidae. Most of them, except for Bombyliidae, Tephritidae, Drosophilidae, Anthomyiidae, and Muscidae, were low-abundant.

Some insects visit the herb-dwarf shrub layer as pollinators. Most of them migrate from the neighboring biotopes on mineral soils. In this group, certain solitary and social bees, syrphid flies, and some wasp-like hymenopterans should be mentioned.

Table 2. Taxonomic composition of insects (Insecta, Ectognatha) in the herb-dwarf shrub layer of peat bogs in Belarus

Taxon	Number of species						
	LZ	PB	HOL	HUM	OBS	L	D
Dictyoptera	1	1	–	1	1	1	1
Orthoptera	7	4	4	2	2	4	4
Psocoptera	1	2	1	2	2	–	2
Sternorrhyncha	4	10	3	9	8	–	7
Auchenorryncha	31	31	22	28	29	16	20
Heteroptera	36	54	20	38	66	23	40
Coleoptera	77	96	44	83	94	44	57
Neuroptera	1	5	–	4	4	–	3
Hymenoptera	4	8	4	8	3	–	6
Diptera	41	42	38	38	45	43	26
In total	**203**	**253**	**136**	**213**	**254**	**131**	**166**

LZ, lagg zone; PB, sphagnum pine bogs; HOL, hollows; HUM, hummocks; OBS, open bogs on the slope; L, lakeshores; D, open biotopes on the dome.

Due to the need for active flying, many of them are not numerous in the quantitative records. We identified 28 species of syrphid flies (family Syrphidae) and 19 bee species (family Apidae). Several species are distinguished among syrphids based on their occurrence: *Sphaerophoria interrupta* (Fabricius, 1805), *S. scripta* (Linnaeus, 1758), *Melanostoma mellinum* (Linnaeus, 1758), and *Eristalis lineata* (Harris, 1776) (Suchko, 2012b). Among bees, *Apis mellifera* Linnaeus, 1758 was the dominant species. The following bumblebees were also common: *Bombus muscorum* Linnaeus, 1758; *B. pascuorum* Scopoli, 1763; *B. hortorum* Linnaeus, 1761; *B. pratorum* Linnaeus, 1761; and *B. jonellus* Kirby, 1802 (Sushko, 2012b).

It is reasonable to identify some specimens from the collections as sustinets (visitors). These are mayflies, caddis flies, and dragonflies. They use the herb-dwarf shrub layer for rest during flying migrations, reproduction, or hunting. These species were not taken into account during the analysis of entomological complexes confined to the herb-dwarf shrub layer, similarly to representatives of the family Aphididae (order Sternorrhyncha). The latter are collected using special methods and occur in aggregations.

Species richness and relative abundance of insect communities in various biotopes. Representatives of ten orders of insects were registered in the herb-dwarf shrub layer of most habitats. The exception is the hollows and lakeshores, where insects of eight and six orders were detected, respectively. Representatives of four orders, which dominate both based on abundance and species richness, constitute the basis of entomological complexes: Coleoptera, Diptera, Heteroptera, and Auchenorryncha. Beetles prevailed in all areas based on the number of species, except for the lakeshores, where dipterans prevailed. The latter were on the second place in the hummock–moss complexes and in the cotton grass–sphagnum associations of the margin. In the remaining biotopes, the second place was occupied by hemipterans (Table 2).

The faunistic situation in the communities was formed by beetle species such as Chrysomelidae (12–34 species); Curculionidae (4–18 species) and Cantharidae (5–14 species) ranked second. Among bugs, the family Pentatomidae (8–11 species) was dominant; Miridae (5–14 species) and Lygaeidae (3–13 species) ranked second. Among cicadas, Cicadellidae prevailed (11–21 species). Among dipterans, 23–24 species were found in all communities.

The highest species diversity was registered in the open biotopes of the slope (262 species) and sphagnum pine bogs (255 species). In the hummocks, the number of species was slightly lower (215). The lowest number of species was found along the lakeshores (134 species) and hollows (139 species) (Table 2).

The same biotopes had the lower relative abundance of insects. On the other hand, the lagg zone, open dome, and sphagnum pine bogs are characterized by a higher relative abundance (Table 3).

If we take into account the distribution of species based on their relative abundance in each order, it is characterized by the dominance of 2–8 species living in various biotopes. For example, the percentage of *Neophilaenus lineatus* (Linnaeus, 1758) among Auchenorryncha varies from 67.50 to 11.93% in all areas; the proportion of *Stephanitis oberti* (Kolenati, 1857) among Heteroptera and *Lochmaea suturalis* (Thomson, 1866) among Coleoptera is above 20% in certain entomological complexes. Besides the above-considered species, this list includes *Cixius similis* Kirschbaum, 1868; *Lepyronia coleoptrata* (Linnaeus, 1758) (Auchenorryncha); *Lygus pratensis* (Linnaeus, 1758); *Kleidocerys resedae* (Panzer, 1797); *Stictopleurus*

Table 3. Registered density of insects (Insecta, Ectognatha) in the herb-dwarf shrub layer of peat bogs of Belarus based on entomological sweep netting

Taxon	Registered density (ind/50 sweeps)						
	LZ	PB	HOL	HUM	OBS	L	D
Dictyoptera	0.38 ± 0.01	0.62 ± 0.03	–	0.38 ± 0.15	0.31 ± 0.75	–	0.46 ± 0.04
Orthoptera	0.92 ± 0.11	1.31 ± 0.32	1.46 ± 0.05	0.62 ± 0.06	0.54 ± 0.44	0.69 ± 0.03	1.15 ± 0.05
Psocoptera	0.15 ± 0.04	0.92 ± 0.09	0.15 ± 0.11	0.31 ± 0.12	0.31 ± 0.31	0.31 ± 0.03	0.77 ± 0.44
Sternorrhyncha	0.38 ± 0.31	2.62 ± 0.01	0.23 ± 0.03	1.08 ± 0.11	0.77 ± 0.11	–	1.54 ± 0.07
Auchenorryncha	**30.77 ± 0.01**	8.38 ± 0.06	**10.23 ± 0.01**	**13.23 ± 0.45**	**13.69 ± 0.03**	3.46 ± 0.36	**14.08 ± 0.01**
Heteroptera	8.46 ± 0.54	**21.38 ± 0.13**	5.38 ± 0.02	**14.15 ± 0.69**	**18.92 ± 0.02**	9.00 ± 0.05	**19.62 ± 0.01**
Coleoptera	**14.85 ± 0.09**	**29.08 ± 0.08**	**13.23 ± 0.01**	**23.77 ± 0.49**	**23.77 ± 0.12**	**15.92 ± 0.09**	**30.46 ± 0.22**
Neuroptera	0.08 ± 0.05	0.54 ± 0.01	–	0.31 ± 0.73	0.46 ± 0.15	–	0.31 ± 0.07
Hymenoptera	3.38 ± 0.11	5.85 ± 0.01	3.62 ± 0.54	4.15 ± 0.02	4.15 ± 0.53	3.31 ± 0.07	5.23 ± 0.09
Diptera	**30.69 ± 0.07**	**17.46 ± 0.86**	**28.08 ± 0.38**	**16.54 ± 0.02**	**19.08 ± 0.14**	**15.23 ± 0.22**	**14.77 ± 0.11**
In total	**90.08** ± 0.04	**88.15** ± 0.23	**62.38** ± 0.11	**74.54** ± 0.03	**82.00** ± 0.16	**47.92** ± 0.04	**88.38** ± 0.12

LZ, lagg zone; PB, sphagnum pine bogs; HOL, hollows; HUM, hummocks; OBS, open bogs on the slope; L, lakeshores; D, open biotopes on the dome.

crassicornis (Linnaeus, 1758) (Heteroptera); *Cyphon padi* (Linnaeus, 1758); and *Plateumaris discolor* (Herbst, 1795) (Coleoptera). Thus, it follows that the complex of insects in the herb-dwarf shrub layer is based on the limited number of dominant species (see Table 4).

Species diversity. The level of differentiation of α diversity was evaluated using the model groups being mostly confined to the herb-dwarf shrub layer (Orthoptera, Auchenorryncha, Heteroptera, Coleoptera).

The highest species diversity of insects was found in open biotopes of the bog slope (H' = 1.979). The second place is occupied by sphagnum pine bogs (H' = 1.930), followed by insect communities of the hummocks (H' = 1.884) and dome (H' = 1.791). However, the smallest variety, in contrast to the species richness, was revealed in the complex of insects inhabiting the bog margins (H' = 1.509) and the lakeshores (H' = 1.511).

The highest evenness of distribution of species base on their abundance was registered in open bogs on the slope (J' = 0.861). The evenness of other open biotopes—on hummocks (J' = 0.855) and the big dome (J' = 0.851)—is slightly lower. The lowest evenness was found in the margins of bogs (J' = 0.686), where the highest dominance concentration was also observed (D = 0.147). On the other hand, the lowest value of the Simpson index was found in open biotopes on the slope (D = 0.021) and hummocks (D = 0.023) (see Table 5).

The β diversity of insect complexes in the herb-dwarf shrub layer was investigated using cluster analysis and made it possible to differentiate two large groups that combined the most similar entomological complexes (Fig. 3).

The first complex includes insect communities of the shores and hummocks. The second complex involves insects of the sphagnum pine bogs and open bogs on the dome and slope having the lowest degree of similarity with insect communities of the lagg zone (Fig. 3).

Main factors determining the structure and dynamics of the species diversity of insects in the herb-dwarf shrub layer. A regression model (GLM) was used to assess the factors of differentiation of insects in the herb-dwarf shrub layer of different biotopes. As a result, it was revealed that the species composition of higher vascular plants providing a food supply for insects in the layer and the projective cover of dwarf shrubs, which are represented by the largest number of species, have the greatest influence on species richness ($P < 0.05$) (Table 6).

The species diversity of insects depends on the same environmental variables as the species richness. In addition, a dependence on the projective cover of herbs was also revealed; it is negative.

The canonical correspondence analysis (CCA) showed the dependence of the distribution of certain insect species on the environmental factors under consideration. The first two canonical axes (Axis 1 and Axis 2) were analyzed. Accordingly, the proportion of the first and second axes accounts for 50.52 and 12.10% of the dispersion, respectively; the contribution of other axes is lower. The canonical coefficients of connection between species and the environment are high for the first two axes (0.99 and 0.92), which indicates the influence of these environmental factors on the variety of insects (see Table 7).

Floristic richness, as well as projective cover of herbs and shrubs, indicated on the diagram by long

Table 4. Relative abundance of insects (Insecta, Ectognatha) in the herb-dwarf shrub layer of peat bogs in Belarusian Poozer'e

Species	Abbreviation	Biotopes						
		LZ	PB	HOL	HUM	OBS	L	D
Metrioptera brachyptera (Linnaeus, 1761)	*Met bra*	0.00	2.30	1.79	1.95	1.79	0.00	2.40
Mecostethus grossus (Linnaeus, 1758)	*Mec gro*	1.79	0.00	2.49	0.00	0.00	1.95	0.00
Linnaemya vulpina (Fallén, 1810)	*Lin vul*	0.00	0.00	0.00	0.00	2.71	0.00	3.26
Cacopsylla ledi (Linnaeus, 1758)	*Cac led*	0.00	4.03	0.00	1.79	3.56	0.00	3.30
Cixius similis Kirschbaum, 1868	*Cix sim*	0.00	2.77	0.00	2.71	2.94	0.00	2.20
Ommatidiotus dissimilis (Fallén, 1806)	*Oma dis*	1.95	0.00	2.08	2.89	2.83	0.00	2.08
Lepyronia coleoptrata (Linnaeus, 1758)	*Lep col*	4.11	2.49	2.30	3.53	3.22	0.00	3.22
Neophilaenus lineatus (Linnaeus, 1758)	*Neo lin*	5.60	2.64	4.26	3.18	3.71	2.08	4.53
Aphrophora alni (Fallén, 1805)	*Aph aln*	2.20	2.30	0.00	2.30	2.49	0.00	2.30
Philaenus spumarius (Linnaeus, 1758)	*Phi spu*	0.00	1.79	0.00	0.00	1.79	0.00	0.00
Ulopa reticulata (Fabricius, 1794)	*Ulo ret*	0.00	2.83	0.00	1.79	2.08	0.00	3.05
Idiodonus cruentatus (Panzer, 1799)	*Idi cru*	1.79	2.08	2.49	2.08	2.30	1.79	2.30
Cicadula quadrinotata (Fabricius, 1794)	*Cic qua*	1.95	0.00	2.30	0.00	0.00	2.40	1.79
Sorhoanus xanthoneurus (Fieber, 1869)	*Sor xan*	1.95	0.00	1.79	0.00	0.00	0.00	1.79
Stephanitis oberti (Kolenati, 1857)	*Ste obe*	0.00	4.22	0.00	3.81	4.16	0.00	3.99
Lygus pratensis (Linnaeus, 1758)	*Lyg pra*	2.89	3.53	0.00	3.37	3.33	0.00	3.58
Globiceps salicicola (Reuter, 1880)	*Glo sal*	0.00	1.79	0.00	0.00	1.95	0.00	0.00
Nabis ferus (Linnaeus, 1758)	*Nab fer*	1.79	2.40	0.00	2.20	2.30	0.00	2.49
Kleidocerys resedae (Panzer, 1797)	*Kle res*	2.49	3.26	2.08	2.40	2.30	2.71	2.20
Cymus grandicolor (Hahn, 1832)	*Cym gra*	0.00	2.49	2.20	2.30	1.79	4.39	1.79
Rhyparochromus pini (Linnaeus, 1758)	*Rhy pin*	0.00	2.71	1.79	0.00	2.30	0.00	2.30
Stictopleurus crassicornis (Linnaeus, 1758)	*Sti cra*	1.95	3.18	1.79	3.00	3.14	0.00	3.22
Eurygaster testudinarius (Geoffroy, 1785)	*Eur tes*	2.20	0.00	0.00	0.00	0.00	0.00	0.00
Aelia acuminata (Linnaeus, 1758)	*Ael acu*	0.00	2.08	0.00	1.79	1.79	0.00	1.79
Dolycoris baccarum (Linnaeus, 1758)	*Dol bac*	0.00	1.95	0.00	1.79	1.79	0.00	1.79
Cyphon kongsbergensis Munster, 1924	*Cyp kon*	2.08	2.57	2.71	2.49	2.40	2.71	3.00
C. padi (Linnaeus, 1758)	*Cyp pad*	2.40	2.49	3.33	2.20	2.20	2.94	2.30
Actenicerus sjaelandicus (Müller, 1764)	*Act sja*	2.83	0.00	0.00	2.30	2.30	1.79	1.79
Ampedus balteatus (Linnaeus, 1758)	*Amp bal*	0.00	2.08	0.00	1.95	1.79	0.00	1.61
Sericus brunneus (Linnaeus, 1758)	*Ser bru*	0.00	2.20	0.00	1.79	1.79	0.00	2.20
Cantharis quadripunctata (Müller, 1764)	*Can qua*	2.64	2.20	1.79	2.30	2.40	2.08	2.08
Absidia schoenherri (Dejean, 1837)	*Abs sch*	0.00	2.57	0.00	2.40	2.30	2.08	2.49
Chilocorus bipustulatus (Linnaeus, 1758)	*Chi bip*	0.00	2.08	2.20	2.30	2.20	0.00	1.79
Coccinella hieroglyphica Linnaeus, 1758	*Coc hie*	0.00	2.64	0.00	2.71	2.57	0.00	3.30
Plateumaris discolor (Herbst, 1795)	*Pla dis*	2.40	0.00	2.77	2.08	2.08	2.49	0.00
Cryptocephalus labiatus (Linnaeus, I761)	*Cry lab*	0.00	2.08	0.00	2.40	2.20	0.00	2.08
Lochmaea suturalis (Thomson, 1866)	*Loc sut*	2.08	4.28	0.00	3.89	3.93	0.00	4.60
Aphthona euphorbiae (Schrank, 1781)	*Aph eup*	2.30	2.20	1.79	1.79	2.77	0.00	1.79
Limnobaris t-album (Fabricius, 1777)	*Lim t-a*	1.79	0.00	2.08	0.00	0.00	3.97	0.00
Micrelus ericae (Gyllenhal, 1813)	*Mic eri*	0.00	1.79	0.00	0.00	1.79	0.00	2.30
Empis borealis Linnaeus, 1758	*Emp bor*	2.08	2.77	2.40	0.00	2.30	0.00	0.00
Rhamphomyia obscura (Zetterstedt, 1838)	*Rha obs*	3.00	3.05	4.14	2.77	2.40	2.89	3.22
Rh. unguiculata Frey, 1913	*Rha ung*	1.95	1.95	2.64	0.00	1.95	1.79	2.08
Dolichopus annulipes Zetterstedt, 1838	*Dol ann*	2.57	2.49	2.83	2.08	2.20	0.00	2.20
Chamaemyia aestiva Tanasijtshuk, 1970	*Cha aes*	3.50	2.30	3.56	2.71	2.57	2.89	2.94
Sepsis cynipsea (Linnaeus 1758)	*Sep cyn*	2.49	0.00	3.22	1.95	2.30	2.71	1.79
Other		31.4	8.06	37.1	17.9	2.24	56.3	2.19

LZ, lagg zone; PB, sphagnum pine bogs; HOL, hollows; HUM, hummocks; OBS, open bogs on the slope; L, lakeshores; D, open biotopes on the dome.

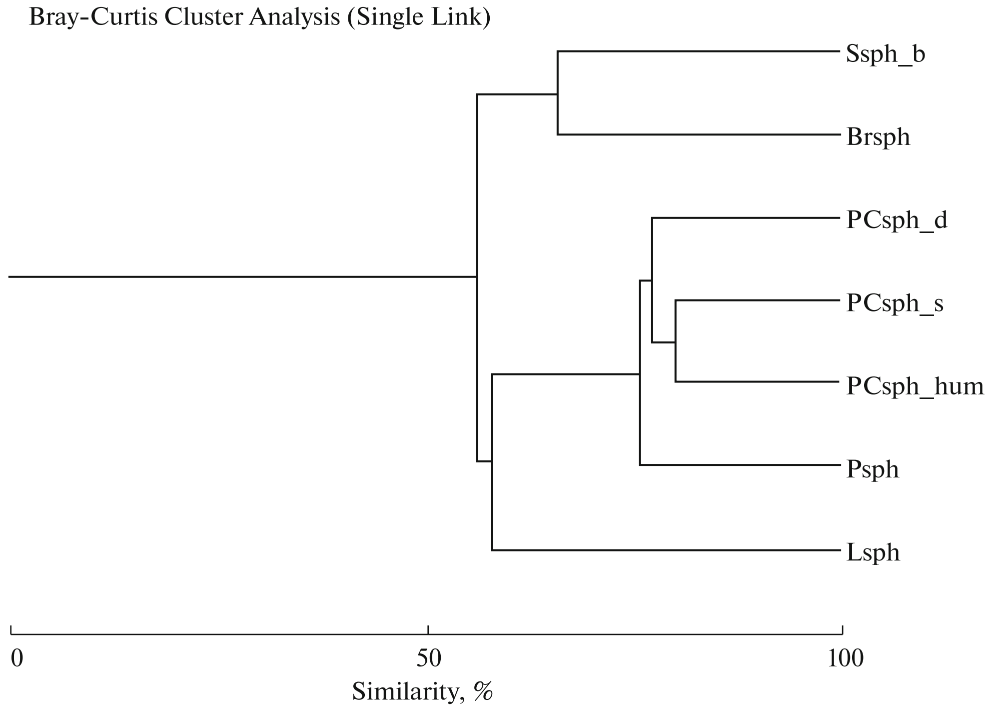

Fig. 3. Dendrogram of similarity between insect assemblages (Insecta, Ectognatha) in the herb-dwarf shrub layer of various biotopes on peat bogs of Belarus based on the quantitative data.

arrows, is most closely related to variations in the species composition and the projective covering of grasses and shrubs. The total projective cover, height of plants, and state of bog waters are of lesser importance (Fig. 4).

Some species have certain points distanced to a varying degree from the vectors corresponding to the environmental variables and are characterized by a different degree of dependence on them. Thus, the projective cover of herbs (PCh) is firstly associated with the distribution of the beetle *Limnobaris t-album* and the locust *Mecostethus grossus* and secondly with the cicadas *Cicadula quadrinotata* and *Sorhoanus xanthoneurus*. The height of plants (HP), which probably determines the light conditions for insects in the layer, is associated with the distribution of *Eurygaster testudinarius* (Heteroptera) and *Plateumaris discolor* (Coleoptera).

An increase in the species richness of vascular plants (RP) and the projective cover of dwarf shrubs (PCsh) is associated with the distribution of *Cacopsylla ledi* (Sternorrhyncha), *Cixius similis, Ulopa reticulata* (Auchenorryncha), *Stephanitis oberti* (Heteroptera), *Lochmaea suturalis*, and *Cyphon kongsbergensis* (Coleoptera). The total projective cover (TPP) influences the spatial distribution of *Aelia acuminata* (Heteroptera) and *Cyphon padi* (Coleoptera).

Many species demonstrate a high degree of dependence on the moistening regime (MDPB). They are *Metrioptera brachyptera* (Orthoptera), *Neophilaenus lineatus, Idiodonus cruentatus* (Auchenorryncha), *Rhyparochromus pini, Cymus grandicolor* (Heteroptera), *Cyphon padi* (Coleoptera), *Rhamphomyia unguiculata, Sepsis cynipsea*, and *Dolichopus annulipes* (Diptera).

The principle component analysis (PCA) showed a clear confinedness of many species to particular habitats and also grouped biotopes in the left and right parts of the ordinal diagram. In one group (to the right), the biotopes dominated by herbs in the projective cover are located; those dominated by dwarf

Table 5. Indices of species diversity for model groups of insects in various biotopes of the herb-dwarf shrub layer on peat bogs of Belarus

Index	LZ	PB	HOL	HUM	OBS	L	D
H'	1.509 ± 0.05	1.930 ± 0.02	1.651 ± 0.03	1.884 ± 0.12	1.979 ± 0.05	1.511 ± 0.04	1.791 ± 0.01
J'	0.686 ± 0.34	0.842 ± 0.08	0.841 ± 0.41	0.855 ± 0.01	0.861 ± 0.09	0.779 ± 0.96	0.851 ± 0.04
D	0.147 ± 0.03	0.026 ± 0.75	0.046 ± 0.05	0.023 ± 0.04	0.021 ± 0.08	0.073 ± 0.06	0.027 ± 0.07

LZ, lagg zone; PB, sphagnum pine bogs; HOL, hollows; HUM, hummocks; OBS, open bogs on the slope; L, lakeshores; D, open biotopes on the dome.

Table 6. Results of regression analysis (general linear model with logarithmic data) of the influence of environmental factors on the species diversity of insects in the herb-dwarf shrub layer on peat bogs of Belarus

Parameter	Coeff.	SE	*t*	*P*
Species richness ($R^2 = 0.586$)				
Species composition of plants	0.057	0.021	2.661	**0.044**
Projective cover of herbs	–0.311	0.183	–1.693	0.151
Projective cover of dwarf shrubs	0.391	0.162	2.413	**0.040**
Total projective cover	0.139	0.086	1.601	0.170
Height of plants	–0.014	0.044	–0.326	0.757
Level of bog waters	0.042	0.101	0.420	0.691
Species diversity ($R^2 = 0.870$)				
Species composition of plants	18.45	3.179	5.802	**0.002**
Projective cover of herbs	–123.2	24.102	–5.113	**0.003**
Projective cover of dwarf shrubs	130.7	21.665	6.034	**0.001**
Total projective cover	19.41	26.492	0.732	0.496
Height of plants	–11.67	10.415	–1.1206	0.313
Level of bog waters	30.47	23.406	1.302	0.249

shrubs are in the second group. The first two axes of the main components (Axis 1 and Axis 2) were analyzed. Accordingly, the first and second axes account for 43.09 and 30.72% of the dispersion, respectively; the contribution of other axes is lower (Table 8). The principle component analysis, which is an indirect gradient analysis (Jongman et al., 1999), showed the important role of vegetation in the spatial distribution of insects in the herb-dwarf shrub layer. On the other hand, the humidification regime is also important, because the points corresponding to the biotopes with greatest moistening (L, HOL, LZ) and the points corresponding to the biotopes with low moisture content (PB, HUM, OBS, D) are located in opposite parts of the ordinal space (Fig. 5).

Hygrophilous hortobionts, some of which are the specialized dwellers of peat bogs (tyrphobionts and tyrphophiles), are highly confined to the biotopes with high bog waters (Spitzer and Danks, 2006).

A clear connection with the margins (LAG) is demonstrated by such tyrphophiles as *Eurygaster testudinarius* (Heteroptera), *Sorhoanus xanthoneurus*, as well as the dominant eurytopic species *Neophilaenus lineatus* (Auchenorryncha). The herb complex along the hollow (HOL) margins are preferred by the tyrphophile *Cicadula quadrinotata* (Auchenorryncha), tyrphobiont *Plateumaris discolor*, as well as the dominant hydrophilous species *Cyphon padi* and *Limnobaris t-album* (Coleoptera), *Sepsis cynipsea* (Diptera), and *Mecostethus grossus* (Orthoptera). Lakeshores (L) covered with *Carex sp*. are mostly associated with moisture-loving dipterans (*Rhamphomyia obscura*, *Rh. Unguiculata*, and *Chamaemyia aestiva*), bugs (*Kleidocerys resedae*), and leafhoppers (*Idiodonus cruentatus*). Open bogs on the slope (OBS) and sphagnum pine bogs (PB) covered with various ericaceous dwarf shrubs are more associated with the tyrphophilous chamebionts *Metrioptera brachyptera* (Orthoptera), *Cixius similis* (Auchenorryncha), *Cacopsylla ledi* (Stenorryncha), *Stephanitis oberti* (Heteroptera), and *Lochmaea suturalis* (Coleoptera). Hummocks and central areas of bogs with relatively low moistening are associated mainly with eurybionts and dwellers of moist meadows, such as *Ulopa reticulata* (Auchenorryncha), (Auchenorryncha), *Stictopleurus crassicornis, Nabis ferus,* and *Lygus pratensis* (Heteroptera) (Sushko and Borodin, 2009; Lukashuk, 2011).

DISCUSSION

Entomological complexes of the herb-dwarf shrub layer consist of insects from the orders Coleoptera, Diptera, Heteroptera, and Auchenorryncha. The faunistic pattern of the layer is made by representatives of families such as Chrysomelidae; Curculionidae and Cantharidae (Coleoptera); Pentatomidae, Miridae, and Lygaeidae (Heteroptera); Cicadellidae and Cer-

Table 7. Canonical coefficients and correlation coefficients of the environment with the first four canonical axes for insect assemblages in the herb-dwarf shrub layer on peat bogs of Belarusian Poozer’e

Indices	Canonical coefficients			
	axis 1	axis 2	axis 3	axis 4
Eigen value	0.29	0.06	0.05	0.03
Dispersion, %	50.52	12.10	9.16	6.80
Accumulated dispersion, %	50.52	62.62	71.79	78.59
Correlation of species and environment	0.99	0.92	0.99	0.94

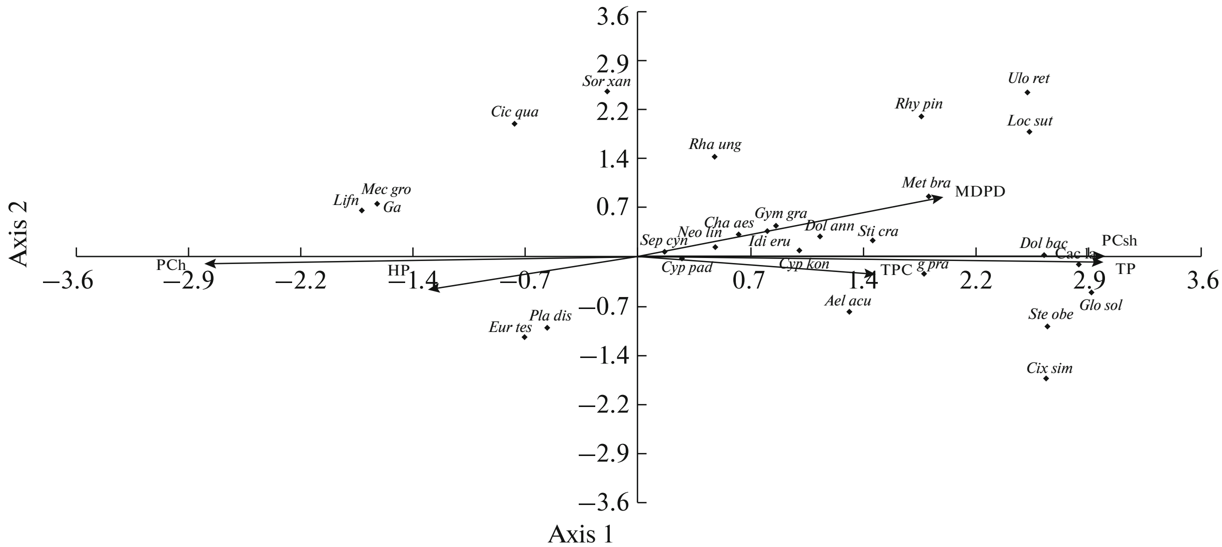

Fig. 4. Ordination diagram of CCA relation between the environmental factors and the species composition of insects in the herb-dwarf shrub layer on peat bogs of Belarus.

copidae (Auchenorryncha); and Chloropidae, Syrphidae, Sepsidae, Dolichopodidae, and Empididae (Diptera).

Despite the smooth gradient of abiotic environmental factors and the mosaic structure and fine contour of plant cover on peat bogs (Boch and Mazing, 1979), the inequivalence of the spatial differentiation was revealed in insect assemblages. The highest species richness is characteristic of sphagnum pine bogs (253 species) and open bogs on the slope (254 species), while lakeshores (136 species) and hollows (131 species) are characterized by the lowest richness. The quantitative parameters of entomological complexes in various biotopes are very similar to the species-richness indices. Thus, a higher abundance of insects was registered in sphagnum pine bogs when compared to hollows and lakeshores. In all biotopes, each order includes two to eight dominants in the orders with highest species richness. However, in most cases certain species are distinguished by especially high abundance. This characterizes peat bogs as extreme ecosystems favorable for a restricted number of species, some of which demonstrate maximum hyperspace seizure in the niche and the usage of the main proportion of resources. According to Thienemann's rule, most species living under extreme conditions are not very abundant, and only some of them with the highest adaptability are numerous. On the other hand, the even distribution of species based on their abundance and their high number characterize the biotope as favorable (Magurran, 1988; Whittaker, 1980).

Table 8. Factor loads on the first four axes for insect assemblages in the herb-dwarf shrub layer on peat bogs of Belarusian Poozer'e

Parameters	Principle component axes			
	axis 1	axis 2	axis 3	axis 4
Eigen value	3.016	2.151	0.631	0.439
Dispersion, %	43.092	30.726	9.016	6.268
Accumulated dispersion, %	43.092	73.818	82.834	89.101

On the whole, the studied insect assemblages are characterized by low α diversity; abundance-based distribution of species; and, as a result, a sufficiently high degree of dominance concentration. The lowest values of species diversity were registered in biotopes with the highest moisture content and the dominance of a single herb species. These are hollows, lakeshores, and lagg zones. On the other hand, the highest species diversity was observed in sphagnum pine bogs and open bogs on the slope, in which the relatively high floristic richness and lower moisture content create optimal conditions for insects. Furthermore, insect assemblages of the biotopes dominated by herbs and dwarf shrubs divided into two groups based on their similarity. Thus, it can be assumed that the main factors of heterogeneity in entomological complexes are moistening regime and vegetation. However, the regression analysis demonstrated that moisture content has no significant influence on biodiversity of insects in the herb-dwarf shrub layer as a whole. At the same time, it determines the spatial distribution of certain species, which was demonstrated by the canonical correspondence analysis. It should be emphasized that the moistening regime is one of the factors determining the biotopical distribution of organisms in the sphagnum layer (Sushko, 2015).

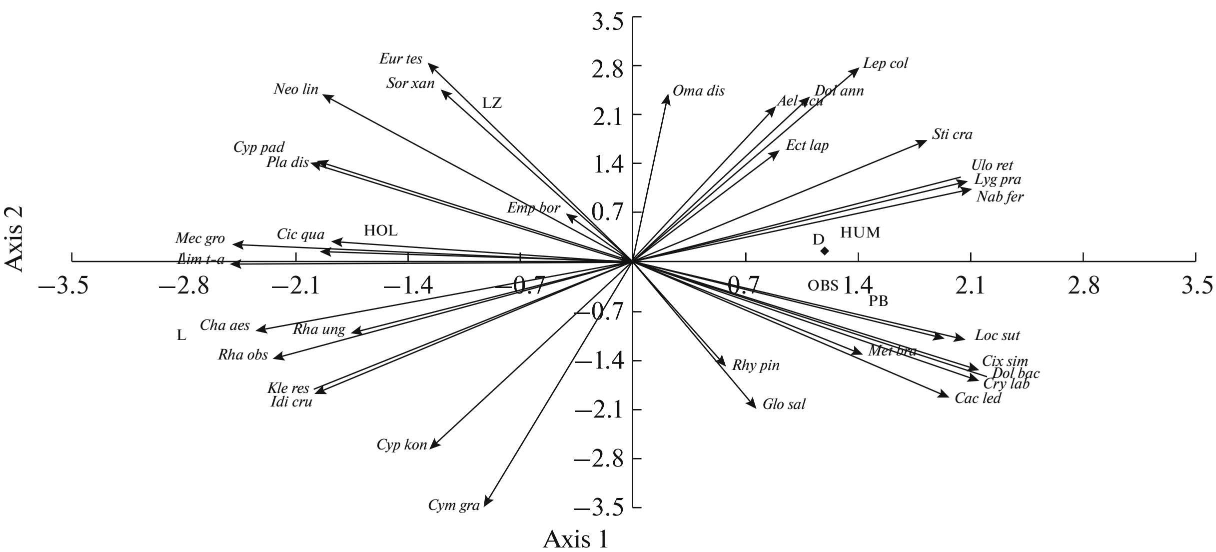

Fig. 5. Ordination diagram of PCA relation between the environmental factors and the species composition of insects in the herb-dwarf shrub layer on peat bogs of Belarus.

In the herb-dwarf shrub layer, the composition of insect assemblages is influenced by the species composition of plants and their projective cover, because they provide insects with food and shelter. On the other hand, they create biotope heterogeneity for insects and, as a result, many species prefer particular ones in the variety on peat bog. This was demonstrated by the principle component analysis.

The comparison of spatial distribution patterns of insects on peat bogs of Belarusian Poozer'e and a number of European regions showed many common features. In Baltic countries, Germany, Poland, and Kalininrad oblast in Russia, the same groups of insects prevail: beetles (leaf eaters and weevils), cicadas, and bugs (Skwarra, 1929; Freese and Biedermann, 2005; Spitzer and Danks, 2006; Spungis, 2008; Nickel and Gärtner, 2009; Rampazzi and Dethier, 1997; Montagna et al., 2008; Friess and Korn, 2013; Holzinger and Schlosser, 2013).

Similar trends were found based a number of aspects in the biotopical distribution of insects between Blarussian Poozer'e and Baltic countries. For example, the highest species diversity among epigenous beetles in Lithuania (Dapkus and Tamutis, 2008) and Poland (Browarski, 2005), as well as all insects in Estonia (Maavara, 1957), was found in sphagnum pine bogs; the least populated were highly moistened hollows. We found such differences for the whole entomological complex.

CONCLUSIONS

Therefore, 374 species from 10 orders were found in the herb-dwarf shrub layer. The studied insect assemblages were based on representatives of the orders Coleoptera, Diptera, Heteroptera, and Auchenorryncha. Each order was dominated by 2–8 species of various biotopes. These are *Cixius similis*, *Neophilaenus lineatusi Lepyronia coleoptrata* (Auchenorryncha), *Lygus pratensis*, *Kleidocerys resedae*, *Stictopleurus crassicornis* (Heteroptera), *Lochmaea suturalis*, *Cyphon padi*, *Plateumaris discolor* (Coleoptera), etc. The highest species richness and relative abundance was revealed in the assemblages of sphagnum peat bogs and open bogs on the slope. Its lowest values were registered in lakeshores and hollows. The entomological complexes were characterized by low diversity, abundance-based distribution of species, and high dominance concentration. The diversity indices characterize the herb-dwarf shrub layer biotopes as extreme and favorable for limited number species.

The lowest values of Shannon's index were obtained in the insect assemblages of hollows, shores, and lag zones. The highest values of this parameter occurred in sphagnum pine bogs and open bogs on the slope. The analysis of β diversity showed a high similarity of the entomological complexes in biotopes dominated by herbs, on the one hand, and dwarf shrubs, on the other. The regression analysis demonstrated significant relations between the species richness and diversity of insects and the species composition of plants and their projective cover. Various methods of multivariate analysis (CCA and PCA) showed the influence of these factors on distribution patterns of particular species and preference given by them to certain biotopes.

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Translated by N. Shulaev